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The genus *Deodrilus*¹⁰ proposed by Mr. Beddard has its sole representative in Ceylon. It seems to combine the character of several of Benham's families, and its exact position is uncertain. Beddard regards it as nearest *Typhæus* and the *Geoscolicidæ*, with some affinities with *Pontodrilus* and many *Eudrilidæ*. Beddard announces a forthcoming classification of the earth-worms.

In the same paper he describes a connection of the nephridia with the terminal region of the intestine as occurring in the New Zealand species *Acanthodrilus multiporus*. These nephridia are connected with the general nephridial network found in the *Plectonephrica*. Whether the portion of the intestine with which they are connected is proctodeal or entodermic is unsettled. Beddard makes some interesting comparisons with the respiratory trees of the *Gephyrea chætifera*, and also with the malpighian tubes of the Hexapods.

THE MECHANICAL ORIGIN OF STRUCTURE IN PELECYPODS.

BY ROBERT TRACY JACKSON.

IT is desired in this paper on Pelecypods to call attention to some cases recently studied in which the structure of the animal seems to be the direct consequence of the physiological reaction induced by the mechanical requirements of the environment; or to cases of "mechanical genesis," as they have been termed.¹ Several of our examples are cases in which similar forms are built up on similar lines of development, but in widely separated or totally distinct groups of animals. They therefore afford evidence

¹⁰ On the Structure of a New Genus of *Oligochaeta* (*Deodrilus*); and On the Presence of Anal Nephridia in *Acanthodrilus*. *Quart. Jour. Mic. Sci.*, XXXI., p. 467, 2 pls., 1890.

¹ This paper is taken largely from a recently published memoir, to which the reader is referred for a fuller discussion of many facts presented. See *Phylogeny of the Pelecypoda, the Aviculidæ and Their Allies*; by Robert Tracy Jackson. *Mem. Bost. Soc. Nat. Hist.*, Vol. IV., No. 8, July, 1890, pp. 277-400, pls. XXIII.-XXX.

in favor of definite lines of variation, and in so far support the view that acquired characters are inherited.

Mr. Wm. H. Dall, in a recent highly interesting paper on Pelecypods, explains the form and progressive development of the ligament, cartilage pit, and teeth of that group as the result of the mechanical strains and stresses to which the parts are exposed.²

In the development of Pelecypods we find in a late embryonic stage (the phylembryonic) that the shell has a straight hinge line. This is characteristic of *Ostrea* (Fig. 1), *Cardium*, *Anodonta*, and so many widely separated genera that it apparently represents a primitive ancestral condition common to the whole class. Embryology shows that the bivalve shell doubtless arose from the splitting on the median line of a primitive univalvular ancestor. If that ancestor had a saddle-shaped³ or a cup-shaped⁴ shell, as is probable, the first result of the introduction of a hinge in the median line would have been to straighten the shell on the hinge line. This is a simple problem in mechanics, for if one tries to break by flexion a piece of metal which is saddle-shaped or cup-shaped, it will tend to form a straight line on the axis of flexion. A parallel case is seen in the development of a bivalve shell in ancient crustaceans. The ancient Ostracoda: *Leperditia*, *Aristozoe*, etc., have a straight hinge line and subcircular valves, which are united dorsally by a ligament. The resulting form of the early

condition of the bivalvular shell in these two distinct classes is so strikingly similar, it lends weight to our supposition that the form is induced by the mechanical conditions of the case.

I think that the adductor muscles which close the valves may also be demonstrated to be the necessary consequence of the bivalvular condition.

FIG. 1.—*Ostrea edulis*, embryo;
a ad, anterior adductor muscle;
m, mouth; a, anus; v, velum; h,
hinge of shell; (after Huxley).

In the phylembryo stage (Fig. 1) the valves are closed by a single adductor muscle, which is the sim-

² On the Hinge of Pelecypods and Its Development, with an Attempt Toward a Better Subdivision of the Group; by Wm. H. Dall. *Am. Jour. Sci.*, Vol. XXXVIII., Dec.,

plest condition mechanically possible to effect the desired end.⁵ This muscle does not seem to be homologous with any muscle in other classes of molluscs, and is probably developed from the mantle muscles as a consequence of the conditions of the case. In support of this view bivalvular crustaceans may again be cited. They have an analogous adductor muscle, developed of course on an entirely different line of descent, but under closely similar mechanical conditions. At the completed prodissoconch stage in all Pelecypods, as far as known, there are two adductor muscles, a second one having developed in the posterior portion of the body. In later life the anterior, the posterior, or both adductors may be retained, reduced, or lost, according as the persistence or changes in correlated anatomical features retain in use or bring into disuse the muscles in question.

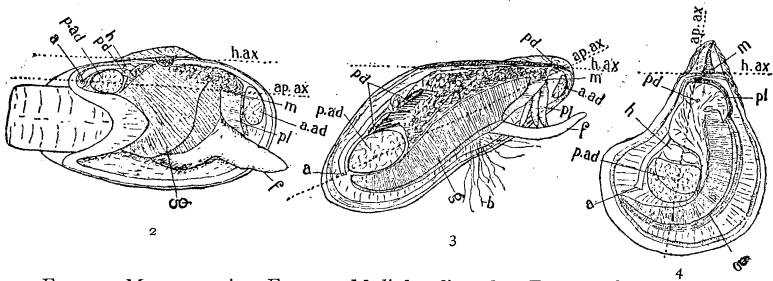


FIG. 2.—*Mya arenaria*. FIG. 3.—*Modiola plicatula*. FIG. 4.—*Ostrea virginiana*. Lettering: *ap ax*, antero-posterior axis; *h ax*, hinge axis; *a ad*, anterior, and *p ad*, posterior adductor muscle; *m*, mouth; *pl*, palps; *a*, anus; *g*, gills; *pd*, pedal muscle; *f*, foot; *b*, byssus; *h*, heart.

Let us look at examples of the retention or loss of the adductors. In typical dimyarian Pelecypods, as *Mya* (Fig. 2) or *Venus*, the adductors lie toward either end of the longer axis of the shell. As the hinge occupies a position on the borders of the shell about midway between the adductors, both muscles are nearly or quite in a position to be equally functional in closing the valves. As

1889. The same author explains graphically on a mechanical ground the origin of structures in Gastropods. See pp. 58-65, Trans. Wagner Free Institute, Vol. III., Aug., 1890.

³ Characteristic of young Dentalium.

⁴ Characteristic of the extreme young of cephalous molluscs.

⁵ This early adductor appears in the same position in many genera, and is apparently characteristic of the class. It is the anterior of the two adductors found in later stages; but it may be retained or lost in the adult.

a result, both muscles are of about the same size. The condition described is that existent in the completed prodissoconch stage in all Pelecypods, as far as known. In later life, however, a revolution of the axes of the soft parts may take place, so that the antero-posterior axis (represented by a line drawn through the mouth and middle of the posterior adductor muscle), instead of being parallel to the hinge axis (the axis of motion of the valves) as in dimyarians, may present a greater or less degree of divergence from the parallel. In progressive series, as in *Modiola* (Fig. 3), *Perna*, etc., as the anterior adductor is brought nearer and nearer to the hinge line, where its mechanical action is less and less effectual in closing the valves, we find that it is more and more reduced until it finally disappears from disuse and atrophy, as in *Ostrea* (Fig. 4), and *Pecten*. Conversely, the posterior adductor in the same series in the revolution of the axes is pushed farther and farther from the hinge line and nearer to the central plane of the valves, where its mechanical action is most effectual in closing the valves. With its increase in functional activity the muscle increases in size. The revolved position of the axes, and the consequent reduction or loss of the anterior adductor and increase of the posterior adductor, is found in many widely separated genera of Pelecypods, as *Ostrea*, *Mulleria* and *Tridacna*; thus proving the development of the same features on different lines of descent.⁶ In *Aspergillum* the two valves have concresced so as to form a truly univalvular, tubular shell, so that the adductors would evidently be functionless if existent. The posterior adductor has disappeared and the anterior is reduced to a few disconnected shreds (Fischer), though evidently existent in the young, as attested by the form of the shell in the nepionic stage.

The condition of the foot in Pelecypods depends largely upon its use or disuse. In free-crawling or burrowing forms the foot is highly developed, and is sometimes of a peculiar form which could doubtless be traced to special functional uses. In *Pecten*, in the nepionic period, the foot is highly developed, and actively

⁶ Dr. B. Sharp and I published almost simultaneously closely similar views on the mechanical aspect of the relative size of the adductors. See *Proc. Acad. Nat. Sci. Phila.*, 1888, p. 122, and *Proc. Bost. Soc. Nat. Hist.*, Vol. XXIII., 1888, p. 538.

employed in crawling. In later stages the animal adopts the habit of byssal fixation, and then of free swimming. The foot becomes highly reduced, and in the adult is probably a functionless organ. In shells which are permanently attached by calcareous fixation the foot is highly reduced or absent, as in *Chama*, *Spondylus*, and *Ostrea* (Fig. 4). In *Ostrea* the shell becomes permanently attached at the close of the free-swimming veliger stage; therefore the foot is unnecessary before fixation and useless afterwards, and it has almost entirely disappeared from even embryonic stages of growth. In *Anomia glabra* the foot is active and well developed in nepionic stages; but later, as the animal becomes permanently attached, it is reduced, and in the adult is highly atrophied.

Ordinarily there are two posterior retractor muscles of the foot in Pelecypods, one situated on either side. In adult *Pecten* either the left retractor alone exists, or both retractors are wanting (the left doubtless always exists in the young). In studies of young *Pecten irradians* I found that the animal always crawled while lying on the right side, with the foot extended through the notch in the lower valve and pressed against the surface of support. It is evident that while crawling in this position the left retractor is in the plane of traction, and it is retained; on the other hand, the right retractor would not be in the plane of traction, and it has disappeared through disuse and atrophy.⁷ A similar disappearance of the right retractors of the foot is seen in *Anomia glabra*, and is explained on similar bases of argument.

The action of the foot in its effect on the form of the shell in some cases presents interesting mechanical features. In dimyarian Pelecypods which crawl freely the foot protrudes from an area on the free border of the valves, nearly opposite to and comparatively far removed from the hinge line. In such cases, by a slight gaping of the valves, a considerable opening is made, through which the foot extends without (ordinarily) the aid of any special notch. On the other hand, in monomyarian Pelecypods, where the revolved position of the axes brings the foot close up to the hinge line, a special notch is required for the extrusion of the foot, as the valves would have to gape very widely to permit of its

⁷ Both retractors probably exist in the prodissoconch stage of *Pecten* and allies.

passage at that area. Such a notch we find in *Tridacna*, *Pecten*, and many allies. Young *Pecten irradians* crawls while lying on its right valve by extending the foot over the edge of the valve. The constant extension of the foot would necessarily cause a local retraction of the right mantle lobe at that area; therefore shell growth would proceed less rapidly, and a notch would consequently be formed. By this action no pressure is exerted on the left mantle lobe, and no notch is formed on that side of the shell.⁸ In later life the crawling habit is abandoned, the foot atrophied, and the notch nearly or quite disappears, as I have observed in several species of *Pecten*. The presence of a byssus at such an area may induce a notch, as well as the crawling habit, as may be observed in *Avicula* and *Meleagrina*. Young *Hinnites* and *Spondylus* are pecteniform and have a deep byssal notch, as I have shown;⁹ but as soon as they become attached by cementation to a foreign object the use of the foot is of course abandoned, and the notch is not perpetuated in succeeding shell growth. In the development of *Anomia* we find that the right valve surrounds the byssus completely, enclosing it at an early stage. In later growth the byssus and calcareous byssal plug become greatly enlarged, the walls of the enclosing foramen receding to give space for the enlargement of the organ. This enlargement of the foramen is apparently to be explained on the physiological principle that constant pressure causes a resorption of tissue.

In free-crawling or superficially burrowing Pelecypods the foot is extended from an area nearly opposite the hinge line, that being the most effectual position for crawling while the valves are in an upright position. In deep-burrowing forms, as *Solen*, on the other hand, the foot is extended at an area nearer the hinge line and in the plane of the longer axis of the shell. It is evident that in this position it is more effectual in producing a hole, it is in a better position to drag the shell after it, and it offers the least resistance to the surrounding medium. In deep burrowers, as *Mya arenaria*, and especially *Ensatella (Solen) americana*, it is to

⁸ For figures illustrating this stage see this journal, December number, page 1138 Figs. 11, 12.

⁹ Phylogeny of the Pelecypoda.

be observed that the borders of the shell gape at either end. This is evidently caused by the constant extension of the foot and siphons, which, pressing on the mantle border, thus keep it back at those areas and modify the direction of shell deposition. Another active cause for the gaping of the valves is doubtless the loss of the habit of withdrawing the organs and closing the valves as a source of protection. Such forms as we are considering are protected in a measure by the surrounding sand or other medium, and in time of danger seek safety by burrowing deeply.

In *Mya arenaria* we find a highly elongated siphon. In the young the siphon hardly extends beyond the borders of the valves, and then the animal lives at or close to the surface. In progressive growth, as the animal burrows deeper, the siphon elongates, until it attains a length many times the total length of the valves. The ontogeny of the individual and the paleontology of the family both show that *Mya* came from a form with a very abbreviated siphon, and it seems evident that the long siphon of this genus was brought about by the effort to reach the surface, induced by the habit of deep burial.

In the structure of *Pecten irradians* we find the most complete adaptation to the mechanical requirements of the act of swimming. *Pecten* swims by the rapid opening and closing of the valves, with the resultant violent expulsion of water; but the details of the method are somewhat intricate. In swimming, as well as when at rest, the left valve is always uppermost, and the plane of the edges of the valves is inclined to the surface of the water at an angle of about 45° . The mantle folds are built up in perpendicular walls on the periphery, and these walls perform an important function in swimming. Lying on the bottom, the *Pecten* suddenly closes its valves by the quick action of the adductor muscle. The first water expelled is driven out posteriorly in the direction of the arrow *a*, Fig. 5, and if this were the only or the main direction in which a current is expelled, the animal would by impact of water be driven in the opposite direction, or anteriorly, which is not the case. When the valves have closed to a slight extent, the borders of the two thick perpendicular mantle walls come in contact, and then no more water is

driven out posteriorly; but instead, during further closure of the valves it is ejected from the lower border of one ear, where the mantle wall is low and thin, in the direction of the arrow *b*. The water expelled at this area is the most forcible current, and is probably of the greatest volume, as by its means the animal is impelled in the opposite direction, as indicated by the arrow *c*. The valves open quickly and clap again. The second time as before the first water is driven out posteriorly; but when the mantle walls come in contact the direction of the excurrent is again changed and it is forced out from the lower border of one ear in the direction of the arrow *d*. Being the strongest current, it impels the animal in the direction of the arrow *e*. At successive claps the water is driven out from alternate ears, as shown in the figure. The resultant action of the several currents and successive claps is to drive

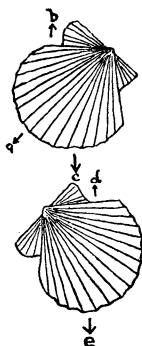


FIG. 5.

the animal in the direction of the free borders of the valves, or posteriorly. It is due to the alternate expulsion of water from either ear, as shown in the figure, that the animal presents a series of zigzag jerks in swimming. The action of the first current expelled posteriorly, before the mantle walls come in contact, gives the animal an upward jerk, and it is in virtue of this jerk, combined with the momentum in a posterior direction, that it maintains its position on the surface of the water, and also the high angle to the surface which it presents in swimming. This current is so powerful that by its action water may be squirted by adults to the height of five inches or more from the surface. In the shell a correlated feature of the swimming habit is seen in the incomplete closure of the valves at the eared areas. Water may therefore pass out when the free borders of the valves are in immediate contact, as they are at each clap, as indicated by the sharp clicking noise made in swimming.

The tendency to equalize the form by growth in a horizontal plane in relation to the force of gravity acting in a perpendicular plane, or the geomalic tendency of Professor Hyatt,¹⁰ is seen mark-

¹⁰ Transformations of Planorbis at Steinheim, with Remarks on the Effects of Gravity upon the Forms of Shells and Animals. Proc. Am. Ass. Adv. Sci., Vol. XXIX., 1880.

edly in Pelecypods. In forms which crawl on the free borders of the valves the right and left growth in relation to the perpendicular is obvious, and agrees with the right and left sides of the animal. In *Pecten* the animal at rest lies on the right valve, and swims with the right valve lowermost. Here equalization to the right and left of the perpendicular line passing through the centre of gravity is noticeable (especially in the *Vola* division of the group); but the induced right and left aspect corresponds to the dorsal and ventral sides of the animal,—not the right and left sides, as in the former case. *Lima*, a near ally of *Pecten*, apparently swims with the edges of the valves perpendicular. In this case the geomalic growth corresponds to the right and left sides of the animal.

The oyster has a deep or spoon-shaped attached valve and a flat or flatter free valve. This form, or a modification of it, we find to be characteristic of all Pelecypods which are attached to a foreign object of support by the cementation of one valve. All are highly modified, and are strikingly different from the normal form seen in locomotive types of the group. The oyster may be taken as the type of the form adopted by attached Pelecypods. The two valves are unequal, the attached valve being concave, the free valve flat; but they are not only unequal, they are often very dissimilar,—as different as if they belonged to distinct species in what would be considered typical forms. This is remarkable as a case of inherited or acquired characteristics finding very different expression in the two valves of a group belonging to a class typically equivalvular. The attached valve is the most highly modified, and the free valve is least modified, retaining more fully ancestral characters. Therefore it is to the free young before fixation takes place, and to the free, least-modified valve, that we must turn in tracing genetic relations of attached groups. Another characteristic of attached Pelecypods is camerated structure, which is most frequent and extensive in the thick attached valve. The form as above described is characteristic of the *Ostreidæ*, *Hinnites*, *Spondylus*, and *Plicatula*, *Dimya*, *Pernostrea*, *Ætheria*, and *Mulleria*, *Chama* and its near allies. These various genera, though ostreiform in the adult, are equivalvular and

of totally distinct form in the free young. The several types cited are from widely separate families of Pelecypods, yet all under the same given conditions, adopt a closely similar form, which is strong proof that common forces acting on all alike have induced the resulting form. What the forces are that have induced this form it is not easy to see from the study of this form alone; but the ostrean form is the base of a series, from the summit of which we get a clearer view.

As I stated in an earlier paper,¹¹ the fullest modification in the ostrean line of variation is the production of a shell in which the attached valve is cup-shaped, conical, or subcylindrical, as seen markedly in species of the Chamidæ and Rudistæ. In this group as a whole, and in progressive stages of growth of its extremest members, all steps may be followed between a simple ostreiform or exogyriiform shell and the most highly modified conical type. The *Ostrea* form is the first step in this line of modification, the *Exogyra* form is the second step, and the conical form is the last step. What are the mechanical causes which bring about this resultant form? I suggest as an hypothesis the following: The Rudistæ are conical or cup-shaped Pelecypods, with a superficially marked radial symmetry. So striking is the radial feature that they have been classed with the corals or Cirripeds, and the term radial is combined frequently in generic and specific names of the group. *Barretia monolifera*, as described by Woodward, is highly radial, and the infoldings of its thin walls closely resemble the radial septa of corals. In other animals which are permanently attached by calcareous fixation, as corals, some worms and Brachiopods, Cirripeds, and others, we find closely comparable forms which are subcylindrical or subconical, with a very marked degree of radial symmetry. Finding so many similar forms built up on different lines of descent affords strong evidence that common forces acting on all alike have induced the resulting form. The equal impact of moving water on all sides of an attached, growing organism, it seems, would cause an equal effort of resistance on all sides, and therefore induce an equal growth on all sides, thus producing a form

¹¹ Studies of Pelecypoda, AMER. NAT., Dec. 1890, p. 1135.

circular in section at any one horizon, and subconical, cup-shaped, or globose in its entirety, as are the forms which we are here considering. To strengthen the walls of a round organism we might have solid accumulation, vesicular accumulation, or perpendicular partitions arranged at right angles to the supported wall. Such mechanical supports are characteristic of attached Rudistæ and other Pelecypods, Cœlenterates, Cirripeds, and some worms. As all sides of the periphery of an attached organism are equally exposed to food supply, danger; etc., the organs, as tentacles, nerve centres, and eyes would gradually tend to become situated at all points on the periphery, or radially. It is well known that the external parts of an animal are more easily modified than the deeper-seated parts. It is also known that the modification of deeper-seated parts may be progressively produced from without inward, or centripetally. If we have an attached animal that is round, with some organs arranged on the periphery, a common case, then further modification or development of such organs or parts would tend to be produced centripetally, or radially, for the centripetal variation of a round form would, as a mechanical necessity, be radial variation. In the Hydrozoa there is a strong proof of the correctness of this view. Passing from Protohydra to Hydra, to the hydroid stage of Aurelia, then to the free medusoid stage of Aurelia and other Discophores, we find progressively a more and more perfect radial symmetry built up centripetally. A similar comparison may be made in the development of corals.

Many permanently attached forms of bilateral classes of animals assume a considerable degree of radial symmetry; and, conversely, many free locomotive forms of radiated classes assume a considerable degree of bilateral symmetry. As bilaterality is a feature induced and progressively built up by the conditions of free locomotion, it is believed that radiality is induced and progressively built up by the conditions of permanent fixation, with its attendant influences of environment.¹²

¹² Since this paper was in type my attention has been called to the fact that Haeckel, in his *Gastræatheorie*, considers the sedentary life of ancestral forms of the zoöphytes as the mechanical efficient cause of their radial symmetry.